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Changes in North Sea macrofauna communities between 1986 and 2000

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Abstract

This paper is chapter 5.2 of the ICES CRR “Structure and dynamics of the North Sea benthos” (ICES 2007) compiled by the ICES Study Group on the North Sea Benthos Project 2000. The North Sea Benthos Project 2000 (NSBP) was initiated as a follow-up to the earlier 1986 ICES North Sea Benthos Survey (NSBS). One major aim of the NSBP 2000 was to compare the outcome with that of the 1986 NSBS, in order to identify any significant changes in the community structure and their likely causes.

In general, the spatial distribution of the macrofaunal communities in 2000 was rather similar to that in 1986. But changes were found within communities which were addressed to changes in the hydroclimate caused by changes in the North Atlantic Oscillation influencing changes in currents and sediment structure as well as food availability.

Keywords: macrofauna communities, long-term variability, NAOI, sediments, North Sea

Introduction

Data sets covering the whole North Sea are very limited. For the infauna, one data set available is the North Sea Benthos Survey (NSBS) in April/May 1986 initiated by the ICES Benthos Working Group (Künitzer et al. 1992, Heip & Craeymeersch 1995, Craeymeersch et al. 1997). The data from surveys during the years 1980 to 1985 in the northern North Sea by Basford & Eleftheriou (1988), Eleftheriou & Basford (1989) and Basford et al. (1990, 1993) were integrated in the NSBS. The North Sea Benthos Project (NSBP) 2000 was initiated as a follow-up to the earlier 1986 NSBS. One major aim of the NSBP 2000 was to compare the outcome with that of the 1986 NSBS, in order to identify any significant changes and their likely causes. Thus, the 1986 data were re-analysed and compared with the 2000 data and possible causal factors for observed differences are discussed.

Methods

Most stations were sampled with a 0.1 m² van Veen grab. Two replicates were taken per station. Part of the samples were taken with a Hamon grab or a box corer (see van den Berghe 2007). The samples were washed over 1 mm mesh size and fixed in 4% formalin. Although a quasi-synoptic sampling was intended for the late spring to early summer season in 2000, data e.g. for the northern parts and the British Channel were only available for the 2001 (see van den Berghe 2007).

For all analyses only NSB data for the nearest matching stations in 1986 and 2000 were used (Fig. 1). Thus, after excluding stations with a distance apart of more than 40 km, 156 matching stations were considered in the analyses. Instead of using the published results of the 1986 data (Künitzer et al. 1992) they were re-analysed since both datasets (1986 and 2000) had to be taxonomically adjusted to allow comparisons.

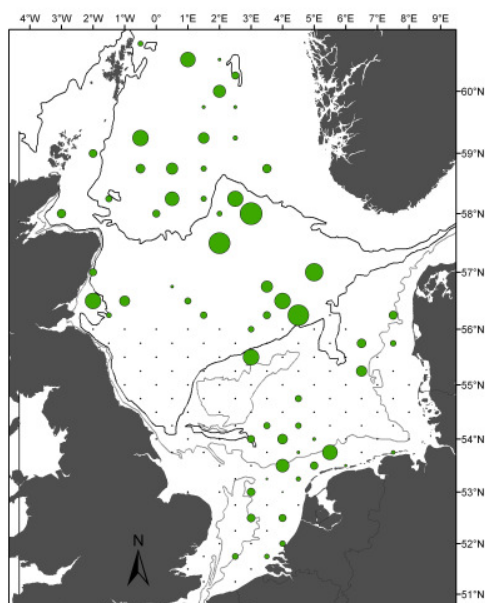


Fig. 1: Location of matching stations with distances apart superimposed (m).

We used the PRIMER v5 program package to perform cluster analysis and multidimensional scaling for abundance data to reveal similarities between stations (Clarke & Warwick 1994). Similarities were calculated using the Bray-Curtis coefficient. Fourth-root transformation was used prior to computation. Similarity percentage analysis (SIMPER) was used to identify species which were mainly responsible for differences in community structure. The significance of any differences in community structure at stations from 1986 and 2000 was tested with ANOSIM. The Hurlbert Index (Hurlbert 1971) was calculated as an expression of species diversity.

The comparison between the univariate parameters and community structure of 1986 and 2000 was carried out using the clusters of 1986 as a starting point. Thus, stations within each of the 1986 clusters were compared with the matching stations sampled in 2000. Additionally, the datasets of 1986 and 2000 were combined in one cluster analysis to detect differences in the cluster classification. If matching stations for both years belonged to one sub-cluster we assumed a consistent classification.

Results

Figures 2 a and b show that the spatial distribution of the macrofaunal communities in 2000 was broadly similar to that in 1986 described by Künitzer et al. (1992). The comparison of the similarity matrices revealed a significant relationship between 1986 and 2000 data (Table 1). The major divisions in the communities of the North Sea still occur at the 50 and 100 m depth contours. Also, greater heterogeneity of communities in the southern North Sea (<50 m) compared to the north is still evident.

Table 1. Correlation coefficients (Spearman rank) relating the similarity matrices of 1986 and 2000 infauna data for different transformation types (RELATE).

	R^2	p
Fourth root	0.533	0.001
Square root	0.527	0.001
Presence-absence	0.511	0.001
No transformation	0.421	0.001

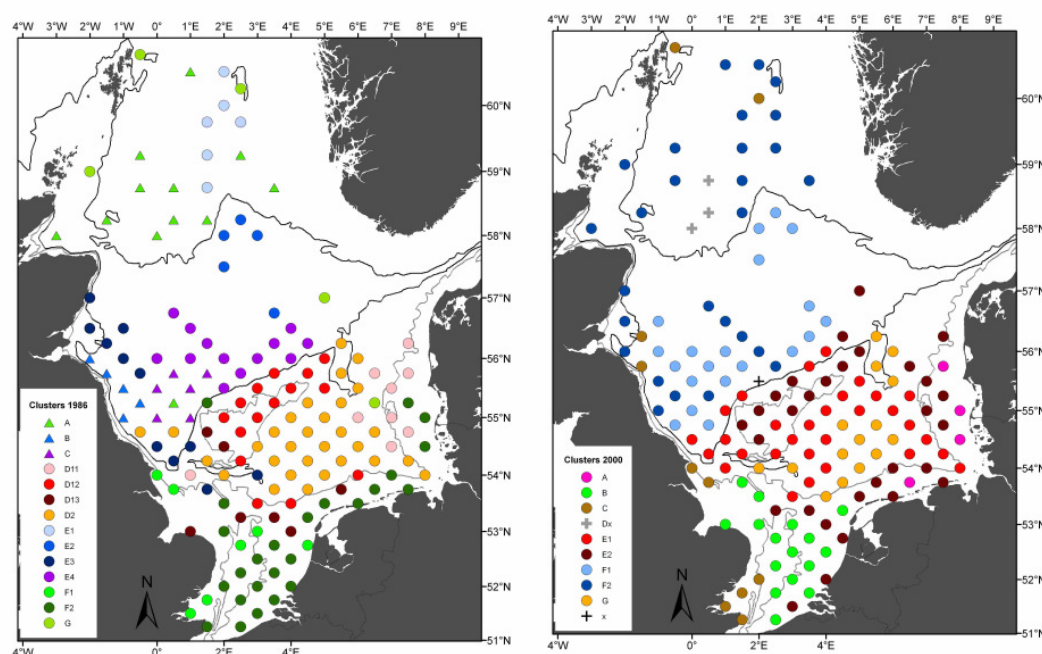


Fig. 2: Spatial distribution of infaunal communities in 1986 (left) and 2000 (right) based on fourth-root transformed abundance data

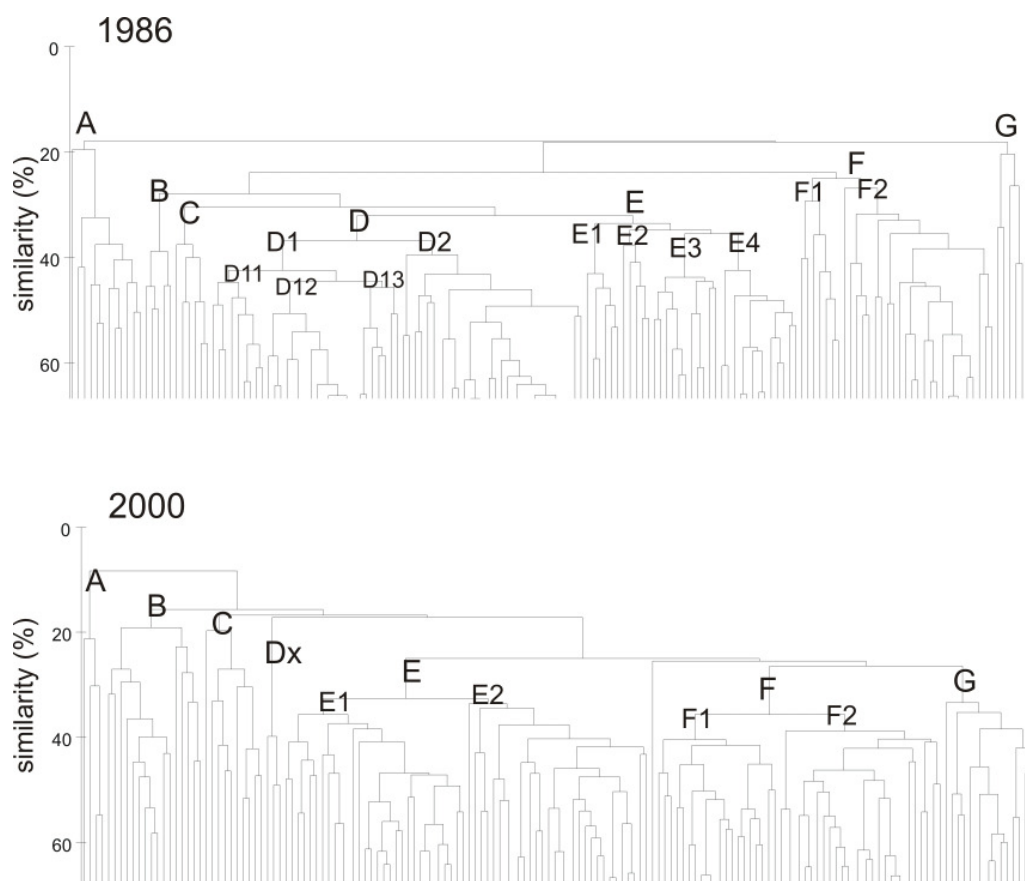


Fig. 3: Cluster dendrograms and groupings shown in Fig. 2 revealed with fourth-root transformed abundance data.

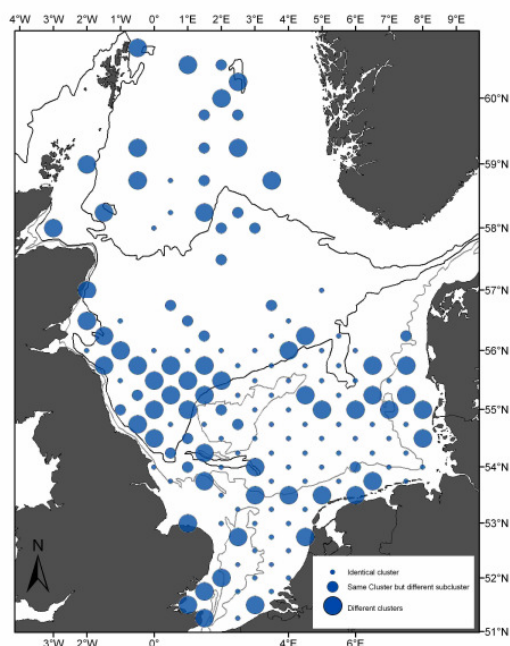


Fig. 4: Distribution of differences in the cluster classification between 1986 and 2000 based on fourth-root transformed abundance data. Small-sized circles represent stations which were classified identically in 1986 and 2000. The largest circles represent stations classified in different main clusters.

However, on closer inspection, there are noticeable differences between the community structure in 1986 and 2000 in some areas of the North Sea. An evaluation of differences in the composition of stations within similar clusters in 1986 and 2000 shows that these were greatest in the eastern North Sea, along the Frisian Front, towards the English Channel, and especially at depths of >50 m off the northern British coast and at >100 m in the northern North Sea (Fig. 4). These have been caused by differences in abundance and species numbers.

Deeper than 100 m, differences in community structure occurred mainly due to a decrease in abundance but an increase in species numbers (Fig. 5). In 2000, the community structure was similar to that in the central North Sea at 50-100 m depth (Fig. 1). But at some of the stations the small polychaet *Paramphinome jeffreysii* occurred in significant densities.

The differences in community structures off the northern British coast (>50 m) seem to be caused by a general decrease in species numbers in parallel with an increase in abundance in 2000 (Fig. 5). In 1986, this area was split into several clusters (mainly B, C, E4), while in 2000 the area was separated mainly into the two clusters F1 and F2 (Fig. 2). The SIMPER analyses show that the differences in community structure have been caused by an increase in the small polychaete *P. jeffreysii*, the interface-feeding polychaetes *Myriochele* spp. and *Spiophanes bombyx* (Fig. 6, Annex 1).

In the eastern North Sea, differences in 2000 occurred due to an increase in abundance of Phoronida and *S. bombyx* and of the bivalves *Fabulina fabula* and *Corbula gibba*, the amphipod *Urothoe poseidonis* and the brittle star *Acrocnida brachiata*.

In the SW North Sea towards the English Channel, both a decrease and increase in species numbers as well as an increase in abundance occurred between 1986 and 2000. At the offshore stations, differences in communities occurred due to an increase in the polychaetes *S. bombyx* and *Magelona* spp., but a decrease in e.g. *Ophelia borealis*. At the coastal stations, the abundance of the polychaetes *Lanice conchilega*, *S. bombyx* and *Lagis koreni* as well as the bivalve *Spisula* spp. increased significantly.

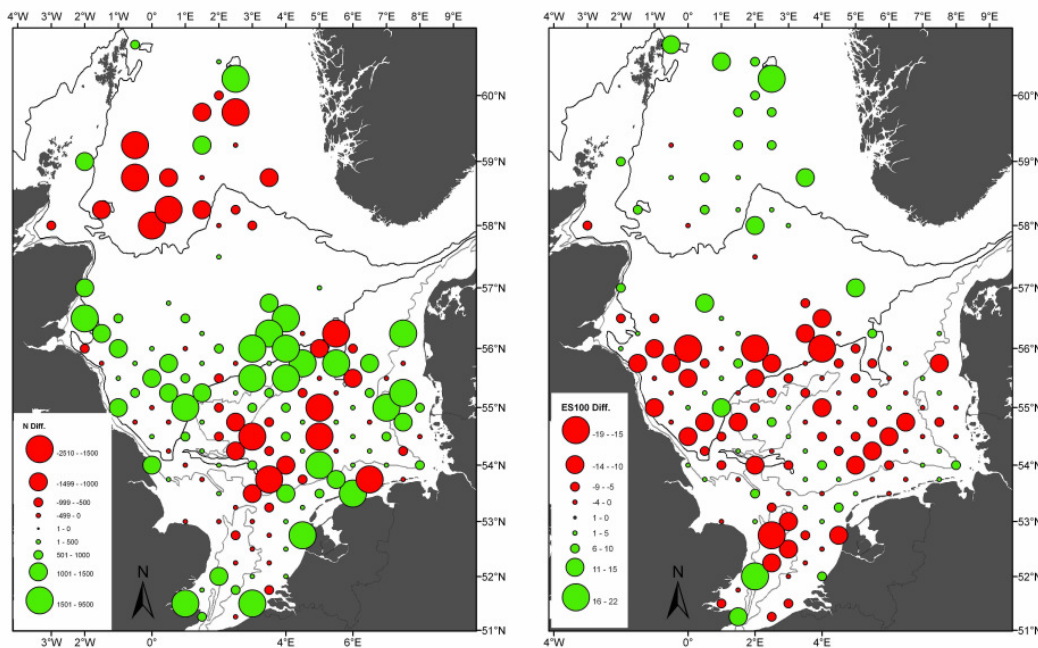


Fig. 5: Differences in mean abundance (left) and mean ES(100) (right) between 1986 and 2000. Green dots indicate an increase and red dots a decrease in 2000 compared to 1986.

At the western part of the Frisian Front differences in community structure could be explained by a general decrease in abundance, e.g., in the polychaete *O. borealis*, while at the eastern part and at the East Frisian coast total abundances increased due to increases in *S. bombyx* and *Magelona* spp. (Fig. 6).

The community structure in the central Oyster Ground remained rather stable over time, but a decrease in total abundance was found at some stations. Also the Dogger Bank community remained rather stable, even if the abundance of the polychaetes *O. borealis* and *Nephtys cirrosa* and the bivalve *Abra prismatica* decreased. At the Tail End abundances of *L. conchilega* and *S. bombyx* increased, while at the South West Patch *Magelona* spp. and *S. bombyx* increased but *Bathyporeia* spp. decreased.

Table 2 reveals that all of the changes in community structure evident from Figure 6 are significant ($p < 5$). An additional contribution to the apparent decline in species number at many stations in the southern North Sea (Fig. 5) may be the use of deeper-penetrating box core samples in 1986. Stations in 2000 were sampled mainly by 0.1m² van Veen grabs.

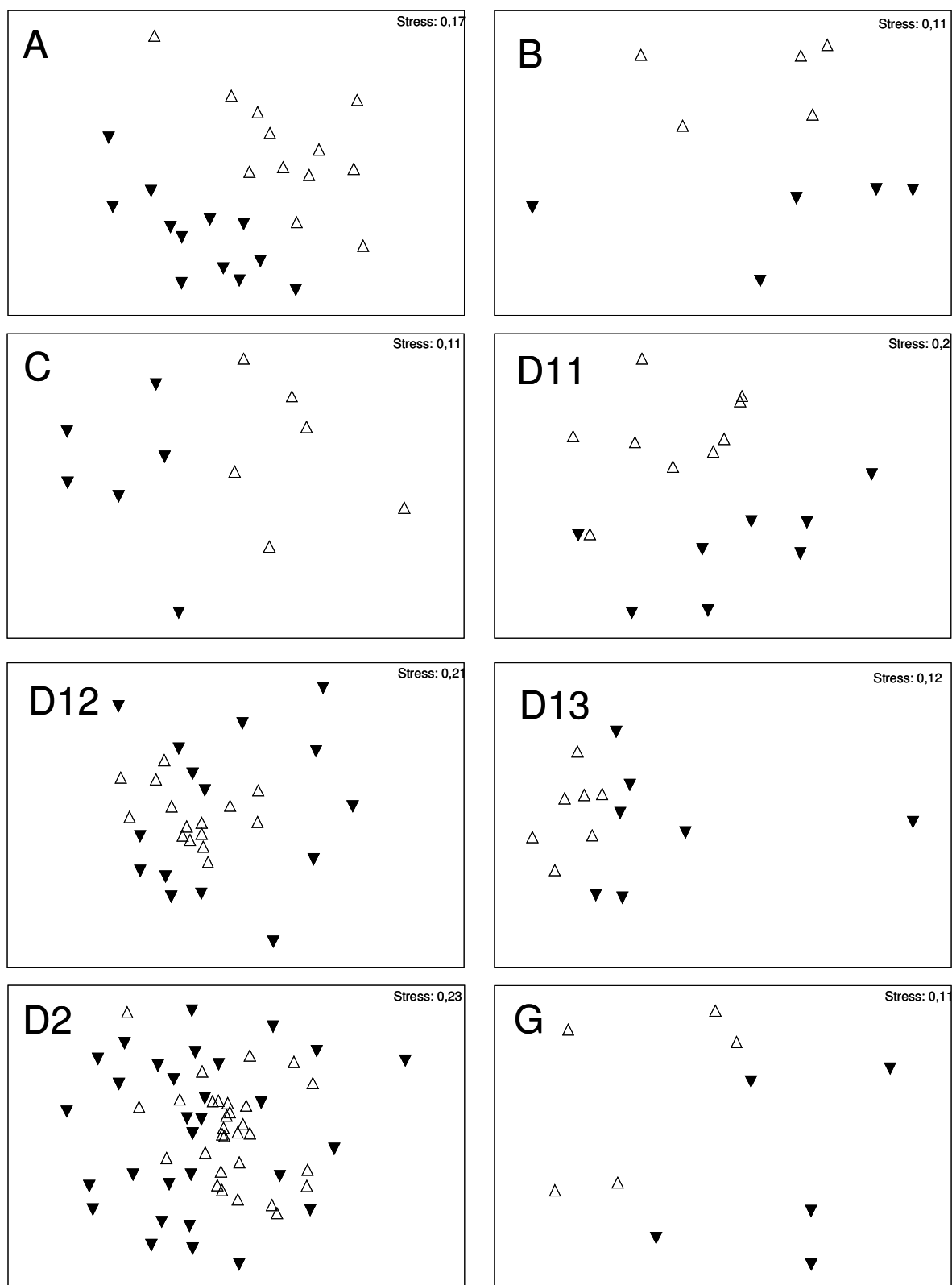


Fig. 6: MDS-plots revealed with fourth-root transformed abundance data of 1986 (\triangle) and 2000 (\blacktriangledown) for the stations of each cluster (see Fig. 3).

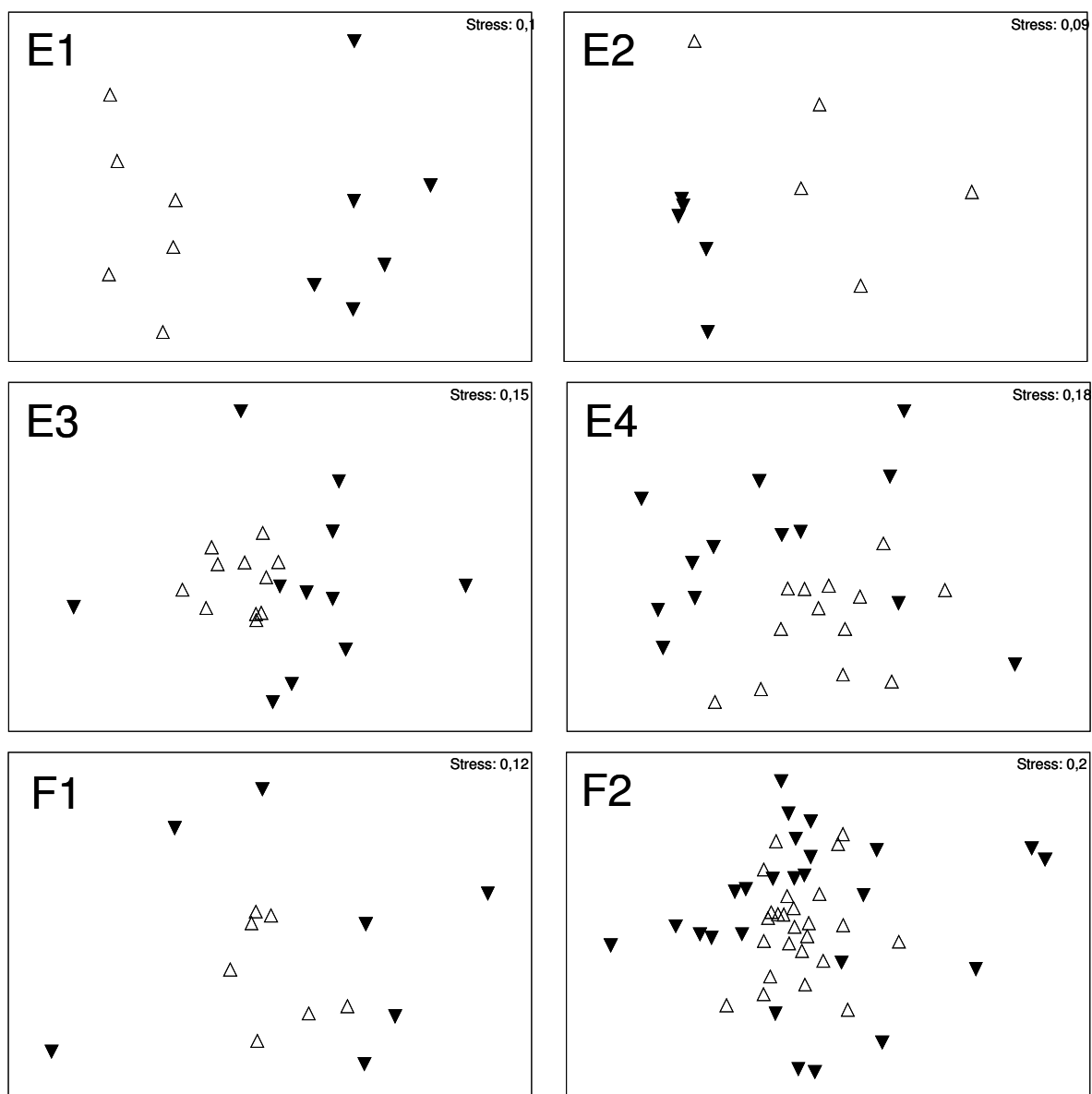


Fig. 6 (continued).

Detailed maps comparing species distribution in 1986 and 2000 are given by Eggleton et al. (2007). van Hoey et al. (2007) and Willems et al. (2007) present detailed correlations of faunal and environmental parameters.

Table 2: Differences between 1986 and 2000 data revealed with ANOSIM for the MDS-plots shown in Figure 6.

Cluster	R	p (%)
A	0.511	0.1
B	0.426	1.6
C	0.648	0.2
D11	0.320	0.2
D12	0.241	0.1
D13	0.190	3.8
D2	0.181	0.1
E1	0.837	0.2
E2	0.588	0.8
E3	0.372	0.1
E4	0.377	0.1
F1	0.202	4.2
F2	0.131	0.1
G	0.404	3.2

Discussion

In general, the spatial distribution of the macrofaunal communities in 2000 was rather similar to that in 1986 described by Künitzer et al. (1992). The major divisions in the structure of the communities of the North Sea still occur at the 50 and 100 m depth contours, as also described by Glemarec (1973).

The decrease in total abundance found in the northern North Sea (>100 m) was caused by the use of different mesh sizes in 1986 (0.5 mm) and 2000 (1 mm) as well as by the spatial resolution of the station grid (Fig. 1). The increase in species number in this region in 2000 might be due to improved taxonomic precision.

Thus “real” changes in community structure between 1986 and 2000 can be more confidently discussed for the southern North Sea. Changes in community structure north of the 50 m depth contour may be related to changes in the hydroclimate caused by changes in the North Atlantic Oscillation which, in positive mode, results in an increase in SST, changes in sediment structure and food availability as described by Reid & Edwards (2001) and Kröncke et al. (1998). Wieking & Kröncke (2001) described the NAO-influenced changes in hydrography especially north and south of the Dogger Bank. The increase in

inflow of Atlantic water masses through the Fair Isle channel strengthened the frontal system north of the bank, which follows the 50 m depth contour, creating a “strong” border between northern and southern water masses. High current velocities in the northern part of the Dogger Bank (Siegismund & Schrum 2001) in addition to a seasonal jet (Brown et al. 1999) limit the accumulation of particulate organic material in seabed sediments. Klein et al. (1999) showed that during storms fine sediment at the sea bed are mobilised at up to 60 m depth at the northern slope of the Dogger Bank. Thus, the decrease in total species number and the increase in species such as the small polychaete *Paramphinome jeffreysii*, as well as the dominance of the interface-feeding polychaetes *Myriochele* spp. and *Spiophanes bombyx* north of the 50 m depth contour, provide supporting evidence for a change in hydrodynamics affecting sediment structure and stability. Since *P. jeffreysii* and *Myriochele* spp. are considered to be cold-temperate species, their increase in abundance north of the 50 m depth contour might be a hint of colder northern water masses north of the frontal system.

Changes observed in the communities at the offshore stations in the SW North Sea towards the English Channel and the eastern part of the Frisian Front indicate similar environmental influences. The decrease in the polychaete *Ophelia borealis* in these regions (see Eggleton et al. 2007) might be due to an increase in SST, since *O. borealis* is a cold-temperate species, as well as to changes in the sediment composition as found by Wieking & Kröncke (2001) at the Dogger Bank

At the coastal stations in the SW North Sea towards the English Channel and at the western part of the Frisian Front an increase in interface-feeding polychaetes such as *S. bombyx*, *Magelona* spp. and *Lanice conchilega* as well as the bivalve *Spisula* spp. might be caused by a higher food availability at the Flamborough and Frisian Fronts due to an NAO-induced increase in SST and hydrodynamic forces. Due to frontal conditions and enhanced primary production, food supply to the benthos (quality and quantity) will be higher than in non-frontal areas at comparable depths (Duineveld & Boon 2002).

In the eastern North Sea, the increase in 2000 in phoronids and other interface-feeding species such as the polychaete *S. bombyx* and the bivalves *Fabulina fabula* and *Corbula gibba* also indicate an NAO-induced increase in food

availability due to higher primary production in the German Bight as described by Reid et al. (1998) and Reid & Edwards (2001). Current-induced changes in the sediment structure might have caused the increase in the brittle star *Amphiura brachiata* and the sea urchin *Echinocyamus pusillus*, which prefers coarser sediments, but *A. brachiata* is also a warm-temperate species (Wieking & Kröncke 2001). Further investigations of links between benthic community structure and environmental variables, including climatic influences, can be found by van Hoey & Rees (2007) and Willems et al. (2007).

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Table Annex : Results of the SIMPER analysis based on fourth root transformed abundance data (Fig. 3, Chapter 5.2). The 1986 clusters were compared with the corresponding stations in 2000.

Cluster A

Average dissimilarity = 72,50

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Thyasira	346,29	17,53	1,18	1,59	1,62	1,62
Lumbrineris latreilli	25,69	0,00	1,02	2,50	1,40	3,03
Myriochele	165,65	109,06	0,98	1,27	1,35	4,38
Paramphinome jeffreysii	29,88	97,03	0,95	1,45	1,31	5,69
Capitella	124,88	2,33	0,92	0,97	1,27	6,96
Pholoe baltica	74,35	4,56	0,90	1,40	1,25	8,21
Exogone	74,86	2,47	0,84	1,26	1,16	9,37
Aricidea catherinae	66,43	4,92	0,84	1,38	1,16	10,53
Cirrophorus lyra	67,41	1,42	0,83	1,22	1,14	11,67
Amphiura chiajei	2,50	55,75	0,83	1,32	1,14	12,81
Heteromastus filiformis	0,00	45,00	0,78	1,19	1,08	13,89
Pseudopolydora	39,85	2,11	0,76	1,27	1,05	14,94
Prionospio	50,95	15,00	0,76	1,22	1,05	15,99
Caulleriella	50,04	1,86	0,75	1,18	1,04	17,03
Eriopisa elongata	42,33	15,50	0,75	1,32	1,03	18,06
Mendicula ferruginosa	27,63	0,92	0,75	1,29	1,03	19,09
Leucon nasica	44,15	13,50	0,73	1,09	1,01	20,10
Diplocirrus glaucus	18,24	26,44	0,73	1,39	1,00	21,10
Levinsonia gracilis	99,36	37,28	0,71	1,34	0,98	22,08
Amphiura filiformis	30,06	30,17	0,69	1,31	0,95	23,03
Lumbrineris gracilis	0,00	7,69	0,68	1,66	0,94	23,96
Eudorella emarginata	21,05	16,92	0,68	1,20	0,93	24,90
Pectinaria	18,33	17,50	0,67	1,44	0,92	25,82
Glycera lapidum	57,56	2,78	0,66	1,05	0,91	26,73
Urothoe elegans	14,04	8,39	0,62	1,40	0,85	27,58
Spiophanes	91,23	62,69	0,61	1,08	0,84	28,43
Laonice sarsi	33,36	5,44	0,61	1,27	0,84	29,27
Notomastus	30,23	8,50	0,61	1,16	0,84	30,10
Owenia fusiformis	27,60	5,53	0,61	1,19	0,84	30,94
Goniada	19,68	9,03	0,60	1,24	0,83	31,77
Eclysippe vanelli	20,81	1,42	0,58	1,20	0,80	32,57
Nothria conchylega	28,25	0,75	0,58	1,05	0,80	33,37
Aplacophora	0,00	8,56	0,57	1,26	0,79	34,16
Eudorella truncatula	6,67	6,06	0,57	1,26	0,79	34,95

Cluster B

Average dissimilarity = 66,44

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Capitella	41,56	0,00	1,20	2,25	1,81	1,81
Ampharete lindstroemi	0,00	81,13	1,08	1,59	1,63	3,44
Praxillella	6,02	0,00	0,78	2,94	1,18	4,62
Paramphinome jeffreysii	0,66	25,10	0,77	1,47	1,16	5,78
Myriochele	178,86	261,83	0,76	1,60	1,15	6,93
Ampelisca spinipes	43,38	0,67	0,74	1,11	1,12	8,05
Anobothrus gracilis	8,64	2,00	0,72	2,05	1,08	9,13
Glycera rouxi	10,34	1,00	0,70	1,48	1,06	10,19
Thyasira	35,62	16,27	0,70	1,26	1,06	11,25
Levinsonia gracilis	38,88	16,03	0,69	1,25	1,04	12,29
Photis	6,72	0,00	0,63	1,60	0,95	13,24
Diplocirrus glaucus	7,94	19,63	0,63	1,41	0,94	14,18
Cirratulus	0,34	5,83	0,61	1,49	0,92	15,11
Heteromastus filiformis	0,00	17,40	0,61	0,98	0,92	16,03
Nephtys hombergii	12,40	5,33	0,61	1,58	0,92	16,94
Owenia fusiformis	5,36	26,53	0,60	2,03	0,91	17,85
Philomedes globosus	26,44	0,00	0,59	0,87	0,89	18,74
Echinocyamus pusillus	12,66	9,40	0,59	0,99	0,88	19,63
Malmgrenia arenicolae	2,68	0,00	0,57	1,80	0,86	20,48
Harpinia antennaria	6,66	23,13	0,57	1,53	0,85	21,34
Dipolydora flava	3,04	0,67	0,56	1,94	0,85	22,19
Urothoe elegans	4,00	10,50	0,56	1,14	0,84	23,03
Leucon nasica	1,66	17,47	0,56	1,07	0,84	23,87
Nuculoma tenuis	3,68	10,77	0,54	1,38	0,81	24,68
Scoloplos	7,70	1,33	0,53	1,15	0,80	25,48
Terebellides stroemi	8,38	3,83	0,52	1,04	0,78	26,26
Echinocardium flavescens	2,00	0,00	0,52	1,91	0,78	27,05
Diastylis lucifera	0,66	16,50	0,52	0,88	0,78	27,83
Cirrophorus lyra	11,00	7,47	0,52	0,86	0,78	28,61
Prionospio	3,34	7,83	0,52	1,24	0,78	29,39
Ampelisca macrocephala	1,00	6,13	0,52	1,41	0,78	30,16
Notomastus	2,68	11,30	0,51	1,37	0,77	30,94
Amphiura chiajei	0,00	15,50	0,51	0,79	0,77	31,71

Lucinoma borealis	6,42	2,00	0,50	1,32	0,76	32,47
Pectinaria	5,70	26,67	0,50	1,54	0,76	33,22
Scoletoma fragilis	3,66	0,00	0,50	1,14	0,76	33,98
Pholoe baltica	8,34	4,13	0,48	1,29	0,73	34,71

Cluster C

Average dissimilarity = 65,78

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Spiophanes	37,30	348,06	1,55	1,22	2,36	2,36
Phyllodoce groenlandica	0,00	9,72	1,41	3,89	2,14	4,50
Paramphinoe jeffreysii	3,95	23,89	1,30	1,38	1,97	6,47
Myriochele	13,32	60,56	1,22	1,10	1,86	8,33
Ampharete lindstroemi	0,00	7,78	1,18	1,97	1,79	10,12
Mysella	27,82	18,06	1,16	1,43	1,77	11,89
Nucula nitidosa	0,00	15,28	1,14	1,88	1,74	13,62
Nemertina	5,27	16,67	1,14	1,57	1,73	15,35
Chaetozone	0,00	6,67	1,08	2,01	1,64	16,99
Pholoe baltica	7,90	6,39	1,03	1,55	1,56	18,55
Cirratulus	0,00	4,17	1,01	1,96	1,54	20,09
Harpinia antennaria	5,27	21,94	0,96	1,19	1,47	21,56
Abra prismatica	2,63	8,06	0,92	1,21	1,40	22,95
Bathyporeia	14,72	2,78	0,90	1,16	1,36	24,31
Eudorellopsis deformis	39,83	16,39	0,90	1,15	1,36	25,68
Polinices	0,00	4,44	0,88	1,30	1,34	27,01
Hippomedon	0,00	4,17	0,85	1,30	1,30	28,31
Goniada	14,67	15,56	0,84	1,03	1,28	29,58
Nuculoma tenuis	3,95	15,00	0,83	1,09	1,26	30,85
Ampelisca tenuicornis	3,95	4,44	0,82	1,25	1,25	32,10
Levinsonia gracilis	9,32	0,56	0,82	1,05	1,25	33,35
Nephtys hombergii	15,98	6,94	0,82	1,06	1,25	34,60

Cluster D11

Average dissimilarity = 63,22

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Phoronida	141,62	1053,33	2,47	1,09	3,91	3,91
Spiophanes	15,12	164,74	1,78	1,58	2,81	6,72
Chamelea gallina	92,47	10,56	1,64	1,19	2,60	9,32
Hexacorallia	57,51	6,11	1,56	1,20	2,46	11,78
Scoloplos	50,48	10,93	1,45	1,16	2,29	14,08
Bathyporeia	45,49	62,96	1,43	1,16	2,27	16,34
Pholoe baltica	19,12	5,00	1,40	1,50	2,21	18,56
Thracia	1,89	29,67	1,40	1,34	2,21	20,77
Tellina	24,37	82,26	1,39	1,23	2,20	22,97
Glycinde nordmanni	15,10	0,56	1,36	1,44	2,15	25,13
Magelona	161,19	221,70	1,29	0,90	2,04	27,16
Goniada	1,64	26,15	1,24	1,43	1,97	29,13
Urothoe poseidonis	5,89	59,78	1,22	0,95	1,94	31,06
Owenia fusiformis	7,10	18,89	1,20	1,32	1,89	32,96
Amphiura filiformis	18,22	3,89	1,14	1,00	1,80	34,75

Cluster D12

Average dissimilarity = 57,08

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lanice conchilega	4,66	261,58	1,14	1,23	1,99	1,99
Bathyporeia	245,40	229,68	0,99	1,40	1,73	3,72
Amphiura filiformis	70,56	12,34	0,96	1,53	1,68	5,40
Mysella	101,64	24,97	0,95	1,20	1,66	7,07
Nephtys hombergii	32,94	3,16	0,94	1,59	1,65	8,72
Ophiura albida	53,31	4,75	0,91	1,42	1,59	10,31
Spiophanes	172,64	593,01	0,90	1,52	1,58	11,89
Urothoe poseidonis	32,27	52,60	0,89	1,36	1,56	13,45
Scoloplos	31,62	28,33	0,84	1,27	1,47	14,91
Ophelia borealis	28,16	4,01	0,81	1,48	1,43	16,34
Nephtys cirrosa	38,85	6,30	0,80	1,19	1,40	17,74
Abra prismatica	21,04	0,67	0,80	1,60	1,39	19,14
Echinocardium cordatum	15,75	14,36	0,79	1,42	1,39	20,53
Owenia fusiformis	7,86	11,33	0,75	1,72	1,31	21,84
Montacuta	21,39	10,15	0,72	1,21	1,26	23,10
Nephtys longosetosa	10,61	0,89	0,69	1,37	1,21	24,31
Acrocrida brachiata	13,51	23,65	0,69	1,32	1,21	25,53
Chamelea gallina	9,46	3,39	0,66	1,38	1,15	26,67
Arctica islandica	6,63	0,22	0,65	1,47	1,15	27,82
Pectinaria	3,66	23,69	0,65	1,11	1,15	28,97
Dosinia lupinus	6,81	1,71	0,65	1,38	1,14	30,11

Sigalion	11,28	9,39	0,65	1,26	1,14	31,25
Nucula nitidosa	13,99	10,50	0,64	0,94	1,11	32,36
Spio	18,08	11,18	0,62	1,24	1,09	33,46
Abra alba	0,94	84,05	0,62	0,67	1,08	34,54

Cluster D13

Average dissimilarity = 58,82

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Echinocardium cordatum	35,27	11,00	2,08	1,60	3,54	3,54
Urothoe poseidonis	47,64	82,17	1,90	1,47	3,24	6,78
Tellina	160,27	116,25	1,82	1,18	3,10	9,88
Magelona	112,96	296,88	1,70	1,17	2,90	12,78
Montacuta	18,24	0,91	1,65	1,61	2,81	15,58
Nephtys hombergii	12,63	1,39	1,63	1,86	2,77	18,36
Nemertina	59,36	22,14	1,50	1,15	2,55	20,91
Nephtys cirrosa	27,73	17,88	1,47	1,13	2,50	23,41
Spiophanes	38,80	146,17	1,45	1,33	2,46	25,87
Bathyporeia	325,09	114,73	1,39	1,23	2,36	28,24
Scoloplos	17,90	6,88	1,32	1,26	2,24	30,48
Donax vittatus	32,40	2,38	1,24	0,98	2,11	32,59
Spio	3,07	11,50	1,12	1,11	1,91	34,50

Cluster D2

Average dissimilarity = 59,70

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Amphiura filiformis	539,31	410,82	1,16	1,23	1,94	1,94
Mysella	215,87	106,71	1,08	1,21	1,80	3,74
Corbula gibba	4,40	103,17	1,01	1,19	1,70	5,44
Magelona	67,28	55,58	0,94	1,34	1,57	7,01
Myriochele	150,42	135,03	0,93	0,89	1,55	8,56
Ophiura albida	44,05	7,23	0,93	1,26	1,55	10,11
Scoloplos	35,52	14,31	0,88	1,28	1,48	11,59
Phoronida	74,74	64,26	0,84	1,20	1,41	12,99
Nuculoma tenuis	23,86	7,34	0,82	1,33	1,38	14,37
Chamelea gallina	32,31	4,99	0,82	1,23	1,37	15,74
Callianassa subterranea	19,62	15,71	0,80	1,34	1,34	17,08
Spiophanes	39,27	73,46	0,79	1,24	1,32	18,39
Pectinaria	25,85	13,40	0,76	1,25	1,28	19,67
Nucula nitidosa	36,79	47,63	0,73	1,11	1,23	20,90
Pholoe baltica	64,45	49,01	0,73	1,20	1,22	22,12
Montacuta	9,58	8,42	0,71	1,19	1,19	23,31
Eudorellopsis deformis	21,81	10,47	0,70	0,98	1,17	24,47
Gattyana cirrhosa	8,53	14,49	0,69	1,18	1,16	25,64
Chaetopterus	10,67	8,29	0,68	1,23	1,15	26,78
Abra alba	2,20	30,47	0,68	1,03	1,14	27,92
Polinices	13,61	10,70	0,68	1,26	1,14	29,06
Bathyporeia	10,08	9,12	0,67	1,25	1,13	30,18
Harpinia antennaria	32,79	41,90	0,67	1,19	1,12	31,30
Owenia fusiformis	9,28	5,59	0,66	1,19	1,10	32,41
Arctica islandica	7,96	0,00	0,65	1,27	1,09	33,50
Echinocardium cordatum	11,52	12,21	0,64	1,23	1,08	34,58

Cluster E1

Average dissimilarity = 65,54

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Paramphinoe jeffreysii	8,37	127,67	0,98	2,06	1,50	1,50
Echinocardium flavescens	113,73	0,33	0,82	1,46	1,25	2,74
Exogone	59,85	1,67	0,80	1,89	1,22	3,97
Eudorellopsis deformis	105,42	2,67	0,78	1,35	1,20	5,16
Amphiura chiajei	0,00	39,50	0,76	1,66	1,15	6,32
Laonice sarsi	5,03	21,50	0,69	2,34	1,06	7,38
Thyasira	41,50	51,17	0,64	1,27	0,98	8,35
Lucinoma borealis	0,00	10,17	0,61	1,83	0,94	9,29
Philine	36,65	8,67	0,61	1,85	0,93	10,22
Glycera lapidum	23,20	17,17	0,61	1,66	0,93	11,15
Urothoe elegans	11,80	19,67	0,59	1,34	0,91	12,06
Abra prismatica	35,07	1,33	0,59	1,23	0,91	12,96
Lanice conchilega	0,00	15,17	0,59	1,88	0,90	13,86
Pholoe baltica	40,18	7,33	0,59	1,59	0,89	14,76
Pholoe pallida	0,00	12,17	0,57	1,80	0,87	15,63
Nothria conchylega	13,33	3,33	0,57	1,62	0,87	16,50
Aonides paucibranchiata	46,67	14,00	0,57	1,83	0,87	17,37
Terebellides stroemi	0,00	9,33	0,56	1,84	0,85	18,22
Aplacophora	0,00	14,83	0,55	1,21	0,84	19,07

Poecilochaetus serpens	20,17	24,83	0,55	1,12	0,84	19,91
Trichobranchus roseus	0,00	6,00	0,55	2,00	0,84	20,75
Phyllodoce mucosa	13,30	0,00	0,55	1,32	0,84	21,58
Ophiosten affinis	23,20	0,67	0,54	1,35	0,83	22,41
Pectinaria	26,77	51,67	0,54	1,42	0,82	23,24
Scolecopsis	8,37	12,33	0,54	2,01	0,82	24,06
Anobothrus gracilis	8,30	11,67	0,54	1,78	0,82	24,89
Prionospio	126,92	25,67	0,54	1,52	0,82	25,71
Eudorella truncatula	28,32	8,00	0,53	1,19	0,81	26,52
Hexacorallia	26,80	21,67	0,53	1,47	0,80	27,32
Acidostoma	0,00	5,17	0,53	1,97	0,80	28,12
Aricidea catherinae	21,73	6,50	0,52	1,92	0,79	28,91
Chaetozone	28,30	12,50	0,51	1,28	0,78	29,69
Montacuta	1,67	4,33	0,51	2,78	0,77	30,46
Nephtys hombergii	6,67	11,00	0,50	1,45	0,77	31,24
Notomastus	8,37	10,00	0,50	1,58	0,77	32,00
Phoronida	10,00	23,33	0,50	1,39	0,77	32,77
Ampelisca tenuicornis	0,00	9,00	0,50	1,32	0,77	33,54
Sthenelais	16,72	3,33	0,50	1,19	0,76	34,30

Cluster E2

Average dissimilarity = 62,04

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Amphiura filiformis	37,74	113,20	1,45	1,54	2,34	2,34
Myriochele	3,02	232,80	1,16	0,99	1,88	4,22
Ophelia borealis	34,44	0,60	1,12	2,68	1,80	6,02
Mysella	34,56	18,40	1,00	1,71	1,62	7,64
Paramphionome jeffreysii	8,00	24,60	0,94	1,47	1,52	9,16
Phoronida	3,00	20,40	0,93	1,56	1,50	10,66
Unciola planipes	10,04	0,00	0,93	1,74	1,49	12,15
Bathyporeia	87,74	8,00	0,92	1,71	1,49	13,64
Anobothrus gracilis	0,00	4,40	0,87	5,37	1,40	15,04
Sthenelais	1,00	8,20	0,85	2,25	1,36	16,41
Tridonta montagui	24,36	0,80	0,82	1,22	1,32	17,73
Pectinaria	42,68	7,00	0,81	1,99	1,31	19,04
Timoclea ovata	10,04	0,20	0,81	1,68	1,31	20,35
Cylichna cylindracea	0,00	3,20	0,80	3,89	1,29	21,64
Diplocirrus glaucus	0,00	4,00	0,74	1,84	1,19	22,82
Magelona	1,00	6,20	0,73	1,41	1,17	23,99
Phyllodoce groenlandica	0,00	3,60	0,72	1,85	1,17	25,16
Chaetozone	34,42	3,60	0,72	1,34	1,16	26,32
Scaphopoda	7,94	6,40	0,71	1,47	1,15	27,47
Nephtys caeca	5,68	7,60	0,71	1,72	1,14	28,61
Travisia forbesii	14,62	0,40	0,70	1,21	1,12	29,74
Molgula	27,84	0,00	0,69	0,80	1,12	30,85
Nemertina	10,56	15,40	0,68	1,37	1,10	31,95
Hexacorallia	10,44	13,60	0,68	1,24	1,10	33,05
Philine	10,60	1,20	0,67	1,49	1,08	34,13

Cluster E3

Average dissimilarity = 68,78

Species	Group 1986 Av.Abund	Group 2000 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Ophelia borealis	54,80	4,18	1,37	2,08	1,99	1,99
Amphiura filiformis	48,75	65,91	0,93	1,31	1,35	3,34
Spiophanes	34,06	357,00	0,90	1,12	1,31	4,64
Echinocardium flavescens	5,63	0,00	0,85	3,21	1,24	5,88
Echinocyamus pusillus	40,98	17,48	0,84	1,49	1,22	7,10
Cochlodesma praetense	8,55	2,61	0,78	1,72	1,13	8,24
Exogone	29,87	0,91	0,78	1,21	1,13	9,37
Myriochele	7,20	116,36	0,77	1,15	1,11	10,48
Mysella	6,94	35,34	0,76	1,25	1,10	11,58
Ophiura albida	6,20	1,73	0,72	2,00	1,04	12,63
Owenia fusiformis	5,53	29,58	0,70	1,20	1,02	13,64
Bathyporeia	26,40	16,52	0,70	1,30	1,01	14,65
Nemertina	18,72	19,39	0,69	1,22	1,00	15,65
Amphiura chiajei	0,91	29,45	0,68	0,89	0,98	16,64
Hexacorallia	8,66	2,79	0,67	1,34	0,98	17,61
Phoronida	6,92	19,59	0,67	1,14	0,97	18,59
Tellina	17,63	2,06	0,66	1,14	0,96	19,54
Pholoe baltica	14,13	24,48	0,66	1,21	0,95	20,50
Notomastus	1,76	20,24	0,64	1,30	0,93	21,42
Thracia	14,84	4,36	0,61	0,95	0,89	22,31
Harpinia antennaria	1,82	15,70	0,60	1,02	0,87	23,19
Glycera lapidum	5,74	18,76	0,60	1,22	0,87	24,06
Nephtys caeca	2,34	7,88	0,58	1,18	0,85	24,91
Nephtys cirrosa	5,84	1,15	0,58	1,11	0,84	25,75
Chamelea gallina	0,45	13,43	0,58	1,09	0,84	26,59
Eudorellopsis deformis	4,90	5,09	0,57	1,08	0,83	27,42

Dosinia exoleta	4,96	2,00	0,56	1,19	0,82	28,24
Nephtys longosetosa	5,17	1,91	0,56	1,18	0,81	29,05
Polycirrus	2,12	7,94	0,55	1,00	0,80	29,85
Abra prismatica	6,15	5,15	0,55	1,16	0,80	30,65
Magelona	10,91	9,28	0,55	1,08	0,79	31,44
Nephtys hombergii	7,50	8,55	0,53	1,14	0,78	32,22
Aonides paucibranchiata	3,97	3,88	0,53	1,27	0,76	32,98
Lumbrineris gracilis	0,00	36,21	0,52	0,85	0,75	33,73
Sthenelais	2,34	4,04	0,51	1,11	0,75	34,48

Cluster E4

Average dissimilarity = 61,98

Species	Group 1986	Group 2000	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
Paramphnime jeffreysii	1,97	61,28	1,18	1,50	1,90	1,90
Myriochele	132,73	357,13	1,03	1,21	1,67	3,57
Nephtys longosetosa	14,08	1,10	0,87	1,64	1,40	4,97
Spiophanes	46,10	242,87	0,86	1,07	1,39	6,35
Mysella	7,91	16,21	0,85	2,00	1,36	7,72
Echinocardium flavescens	4,65	1,92	0,79	2,28	1,28	9,00
Abra prismatica	8,06	6,67	0,78	1,70	1,25	10,25
Levinsonia gracilis	17,30	19,97	0,76	1,23	1,23	11,48
Polinices	4,02	5,00	0,74	1,83	1,20	12,67
Eudorellopsis deformis	16,10	16,82	0,74	1,21	1,19	13,86
Nephtys hombergii	8,55	1,33	0,72	1,61	1,16	15,02
Chaetozone	4,31	19,41	0,69	1,26	1,11	16,13
Pectinaria	9,18	13,44	0,67	1,17	1,09	17,21
Cirratulus	9,27	3,28	0,65	1,24	1,04	18,25
Hemilamprops rosea	4,13	2,46	0,65	1,66	1,04	19,29
Aplacophora	5,50	6,62	0,63	1,24	1,02	20,32
Montacuta	10,37	3,36	0,63	1,16	1,02	21,34
Ophiocten affinis	6,64	1,03	0,63	1,27	1,02	22,35
Hexacorallia	6,81	24,82	0,62	1,18	0,99	23,34
Prionospio	7,00	6,62	0,61	1,23	0,99	24,34
Phaxas pellucidus	5,80	5,82	0,61	1,22	0,99	25,32
Pholoe baltica	6,30	7,28	0,61	1,17	0,98	26,30
Ampelisca tenuicornis	9,39	5,59	0,61	1,15	0,98	27,28
Magelona	5,62	8,28	0,60	1,05	0,98	28,25
Owenia fusiformis	5,37	2,82	0,59	1,12	0,95	29,20
Westwoodilla caecula	4,45	0,87	0,58	1,26	0,94	30,14
Harpinia antennaria	2,66	6,97	0,57	1,19	0,91	31,05
Diplocirrus glaucus	3,43	5,64	0,55	1,15	0,89	31,94
Synchelidium	0,13	2,85	0,54	1,19	0,88	32,82
Trichobranchus roseus	0,88	5,33	0,54	1,12	0,87	33,69
Hippomedon	2,94	0,67	0,54	1,16	0,87	34,56

Cluster F1

Average dissimilarity = 78,73

Species	Group 1986	Group 2000	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
Pholoe baltica	53,42	16,67	1,29	1,23	1,64	1,64
Lanice conchilega	30,53	531,87	1,28	0,95	1,63	3,27
Capitella	31,17	0,00	1,26	1,82	1,60	4,87
Lumbrineris latreilli	26,71	0,00	1,23	1,18	1,56	6,42
Urothoe poseidonis	114,76	118,22	1,20	0,90	1,53	7,95
Mysella	111,51	39,24	1,16	0,99	1,48	9,43
Nemertina	54,67	27,96	1,14	1,07	1,45	10,88
Mya	22,24	7,14	1,11	1,37	1,41	12,29
Nicomache	122,94	1,90	1,06	1,05	1,35	13,64
Scoloplos	40,10	10,30	1,06	1,17	1,35	14,99
Spisula	1,12	739,56	1,05	0,56	1,34	16,33
Spiophanes	13,11	127,81	1,04	1,07	1,33	17,65
Pectinaria	10,09	226,12	1,04	0,89	1,33	18,98
Hexacorallia	3,46	73,81	0,99	0,95	1,26	20,23
Ophiura albida	19,77	1,90	0,98	1,53	1,24	21,48
Polycirrus	21,09	12,38	0,97	1,14	1,23	22,71
Ampelisca spinipes	18,39	1,90	0,94	1,03	1,20	23,90
Pomatoceros	10,36	77,62	0,93	1,10	1,18	25,09
Chaetozone	9,61	0,91	0,89	1,39	1,13	26,21
Scalibregma	6,76	18,10	0,88	1,16	1,11	27,33
Glycera lapidum	15,36	10,95	0,85	1,35	1,08	28,41
Urothoe brevicornis	25,36	20,16	0,82	0,93	1,04	29,45
Eusyllis blomstrandii	22,68	0,00	0,80	0,98	1,02	30,47
Eumida sanguinea	10,65	9,35	0,79	1,25	1,01	31,48
Malmgrenia arenicolae	10,52	0,00	0,78	0,91	0,99	32,46
Spio	13,95	6,63	0,77	1,10	0,98	33,44
Nephtys cirrosa	7,10	8,73	0,74	1,03	0,94	34,38

Cluster F2

Average dissimilarity = 72,82

	Group 1986	Group 2000				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Spiophanes	22,55	395,85	2,08	1,21	2,85	2,85
Ophelia borealis	44,78	4,28	2,07	1,24	2,84	5,69
Magelona	72,62	118,65	2,03	1,23	2,79	8,48
Scoloplos	46,41	54,78	1,98	1,29	2,72	11,20
Urothoe poseidonis	15,72	57,60	1,73	1,04	2,38	13,58
Tellina	22,01	54,40	1,67	1,05	2,29	15,87
Bathyporeia	47,77	38,10	1,62	1,22	2,23	18,10
Spio	18,85	32,54	1,56	1,12	2,14	20,24
Lanice conchilega	9,53	48,74	1,50	0,99	2,06	22,30
Nemertina	21,02	19,76	1,45	1,17	2,00	24,30
Urothoe brevicornis	24,78	4,72	1,37	0,94	1,88	26,18
Spisula	62,82	3,92	1,35	0,96	1,85	28,03
Nephtys cirrosa	21,94	19,71	1,31	1,11	1,80	29,83
Echinocardium cordatum	11,45	4,93	1,26	1,04	1,73	31,56
Gastrosaccus spinifer	3,15	27,68	1,26	0,76	1,72	33,28
Scoelepis	5,31	6,89	1,23	1,04	1,69	34,97

Cluster G

Average dissimilarity = 80,10

	Group 1986	Group 2000				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Spiophanes	14,26	53,30	1,18	1,43	1,47	1,47
Paramphionome jeffreysii	0,00	246,90	1,11	1,17	1,38	2,85
Aonides paucibranchiata	63,84	19,20	1,03	1,20	1,29	4,14
Magelona	0,00	86,67	1,03	0,65	1,28	5,42
Exogone	90,68	23,60	1,00	1,21	1,25	6,67
Glycera lapidum	76,78	24,90	0,99	1,16	1,24	7,91
Phoronida	0,00	22,90	0,97	0,94	1,21	9,12
Amphiura filiformis	3,42	64,47	0,93	1,12	1,16	10,28
Aricidea cerrutii	44,20	10,00	0,89	1,17	1,11	11,39
Myriochele	1,00	22,10	0,89	1,49	1,11	12,50
Unciola planipes	20,22	7,60	0,86	1,08	1,07	13,57
Harpinia antennaria	0,00	53,60	0,83	0,78	1,03	14,60
Hexacorallia	25,12	14,50	0,82	1,13	1,02	15,63
Scoloplos	14,68	12,33	0,82	1,32	1,02	16,64
Nephtys longosetosa	10,22	0,00	0,80	1,11	0,99	17,64
Scoelepis	12,08	18,10	0,77	1,17	0,97	18,61
Spio	2,00	23,30	0,77	1,14	0,96	19,56
Owenia fusiformis	18,88	14,60	0,76	1,16	0,95	20,51
Ophelia borealis	13,76	1,60	0,76	1,13	0,95	21,46
Corbula gibba	2,00	36,67	0,75	0,63	0,94	22,40
Echinocyamus pusillus	10,96	12,40	0,75	1,18	0,94	23,33
Bathyporeia	11,60	9,87	0,74	0,92	0,92	24,26
Goniada	41,22	21,03	0,74	1,29	0,92	25,18
Dipolydora socialis	11,96	0,00	0,73	1,13	0,92	26,10
Polinices	0,00	7,87	0,73	0,91	0,91	27,01
Pholoe baltica	0,00	9,07	0,72	1,12	0,89	27,90
Pisone remota	14,06	23,60	0,71	0,86	0,88	28,78
Nemertina	7,98	31,93	0,70	1,28	0,88	29,66
Chaetozone	9,46	17,47	0,70	1,15	0,87	30,53
Nephtys hombergii	0,00	5,30	0,69	1,06	0,86	31,39
Hesionura elongata	23,84	0,80	0,67	0,88	0,84	32,23
Spisula	6,42	0,40	0,67	1,08	0,84	33,07
Oligochaeta	0,00	26,00	0,66	0,79	0,82	33,89
Prionospio	2,00	14,10	0,65	1,17	0,81	34,70